The Phylogenetic Position of the Eugaleaspida in China

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Primitive vertebrates from the Middle Silurian and Lower Devonian rocks of China are grouped into a new major taxon, the Eugaleaspidomorphi, equivalent in status to the Cephalaspidomorphi and the Pteraspidomorphi. This is based upon a discussion of the cranial anatomy and the nature of the openings in the well ossified headshield.

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INTRODUCTION

This paper is essentially that read in February 1983 at the Symposium on the Evolution and Biogeography of Early Vertebrates under the sponsorship of The Australian Academy of Science, The Australian Museum and The Association of Australasian Palaeontologists, held in Sydney and Canberra.

Devonian agnathans were first listed from eastern Yunnan Province, south China (Fig. 1) by V. K. Ting and Y. L. Wang in 1937 (Ting and Wang, 1937; Young, 1939). It was not until 1965, however, that the Early Devonian agnathans from eastern Yunnan were first described by Liu Yuhai on the basis of material from near Qujing (Chutsing) (Liu, 1965). For the next eight years there was little new information about the Early Devonian Agnatha in China, until Liu (1973: 133-135) described another genus *Huananaspis,* placed in a new family Huananaspidae. Since then many new agnathan genera have been described (Liu, 1975; P'an, Wang and Liu, 1975; P'an and Wang, 1978; Cao, 1979; Pan and Wang, 1980, 1981; Wang *et al.,* 1980; Wang and Wang, 1982a, b), which may be placed in seven groups, as follows:

Middle Silurian
- Group 1 — Hanyangaspids
  - *Hanyangaspis guodingshanensis* P'an and Liu, in P'an *et al.*, 1975
  - *Latirostrasps chaohuensis* Wang, Xia and Chen, in Wang *et al.*, 1980

Early Devonian (including some in Late Silurian)
- Group 2 — Eugaleaspids
  - *Eugaleaspis changi* (Liu) 1976, emended Liu, 1980
  - *Eugaleaspis xujiachongensis* (Liu) 1975, emended Liu, 1980
  - *Yunnanogaleaspis major* Pan and Wang, 1980
  - *Sinogaleaspis shankouensis* Pan and Wang, 1980
  - *S. xikengensis* Pan and Wang, 1980
- Group 3 — Nanpanaspids
  - *Nanpanaspis microculus* Liu, 1965
- Group 4 — Polybranchiaspids
  - *Polybranchiaspids liaojiaoshanensis* Liu, 1965
  - *P. minor* Liu, 1975

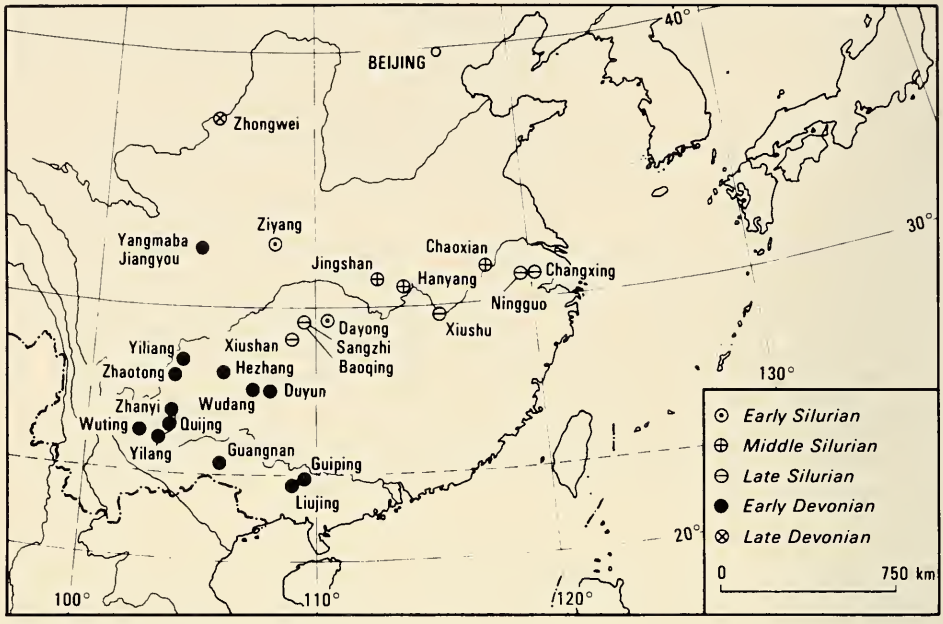

Fig. 1. Localities of Silurian and Devonian Agnatha in China.

P. yulongssus Liu, 1975
P. miandiancunensis P'an and Wang, 1978
P. zhanyiensis P'an and Wang, 1978
Siyingia altuspinosa Wang and Wang, 1982a
Laxaspis qujingensis Liu, 1975
L. rostrata Liu, 1975
Dongfangaspis major Liu, 1975
D. qujingensis Pan and Wang, 1981
Diandongaspis xishancunensis Liu, 1975
Damaspis vartus Wang and Wang, 1982b
Cyclodiscaspis ctenus Liu, 1975
Kwangnanaspis subtriangularis Cao, 1979

Group 5 — Duyunolepids

Duyunolepis paoyangensis (P'an and Wang) 1978, emended Pan and Wang, 1982
Paraduyunaspis hezhangensis P'an and Wang, 1978
Neoduyunaspis minuta P'an and Wang, 1978

Group 6 — Huananaspids

Huananaspis wudinensis Liu, 1973
Asiaspis expansa P'an, in P'an *et al.*, 1975
Sanqiaspis rostrata Liu, 1975
S. zhaotongensis Liu, 1975
S. sichuanensis P'an and Wang, 1978
Sanchaspis magalarostrata Pan and Wang, 1981

Group 7 — Lungmenshanaspids

Lungmenshanaspis kiangyouensis P'an and Wang, in P'an *et al.*, 1975

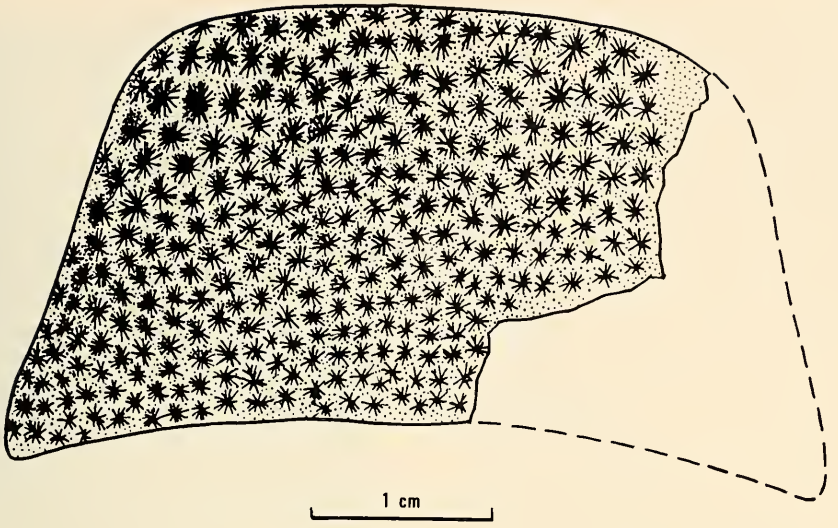

Fig. 2. Latirostraspis chaohuensis Wang, Xia and Chen. An example of the trapezoidal anterior ventral plate (VA001, Museum of Geology, Beijing). Middle Silurian, Fentou Formation, Chaohu, Chaoxian County, Anhui Province.

Sinoszechuanaspis yanmenpaensis (P'an and Wang) in P'an *et al.,* 1975, emended P'an and Wang, 1978
Qingmenaspis microculus Pan and Wang, 1981

Latirostraspis chaohuensis (Wang *et al.,* 1980), a genus within the Hanyangaspidae (P'an, Wang and Liu, 1975) differs slightly from the other members of the group in the shape of the anterior ventral plate (Fig. 2), and in the position of the anterior dorsal median opening.

These various forms, which may generally be referred to as 'eugaleaspidomorphs', include agnathans of varying size. Typically, the anterior portion of the body is covered dorsally and laterally by a single plate, forming the cephalic shield. Along the rostral and lateral margins the cephalic shield is folded ventrally, forming an even, hemicyclic, ventral rim in *Polybranchiaspis liaojiaoshanensis* (Liu, 1975: fig. 5B) and *Asiaspis expansa* (Fig. 3), or an even, ventral rim on either side of which is joined the interzonal part of the cephalic shield in *Hanyangaspis guodingshanensis* (Fig. 5). A section through the posterior part of the cephalic shield in *Asiaspis expansa* is shown in Fig. 3**B.** This genus is similar in several features to the polybranchiaspids, but differs from them in that (a) the rostral process and cornua are well developed, (b) there is a different cross-section of the posterior part of the shield (Fig. 3**B**, **C**), and (c) the shield has a higher lateral wall.

The Eugaleaspidomorphi, proposed here as a new endemic group of Agnatha, are so far only known from Early Silurian (Llandovery) to Late Devonian (Famennian) strata in China (Fig. 1), but very possibly they also occur elsewhere in southeast Asia, such as in Vietnam. Relevant new discoveries in China, not yet described, include polybranchiaspids and hanyangaspids which were recently (1981-82) recovered from an Early Silurian formation in western Hunan Province of south China, and in southern Shaanxi Province, west China. In the same year, many incomplete cephalic

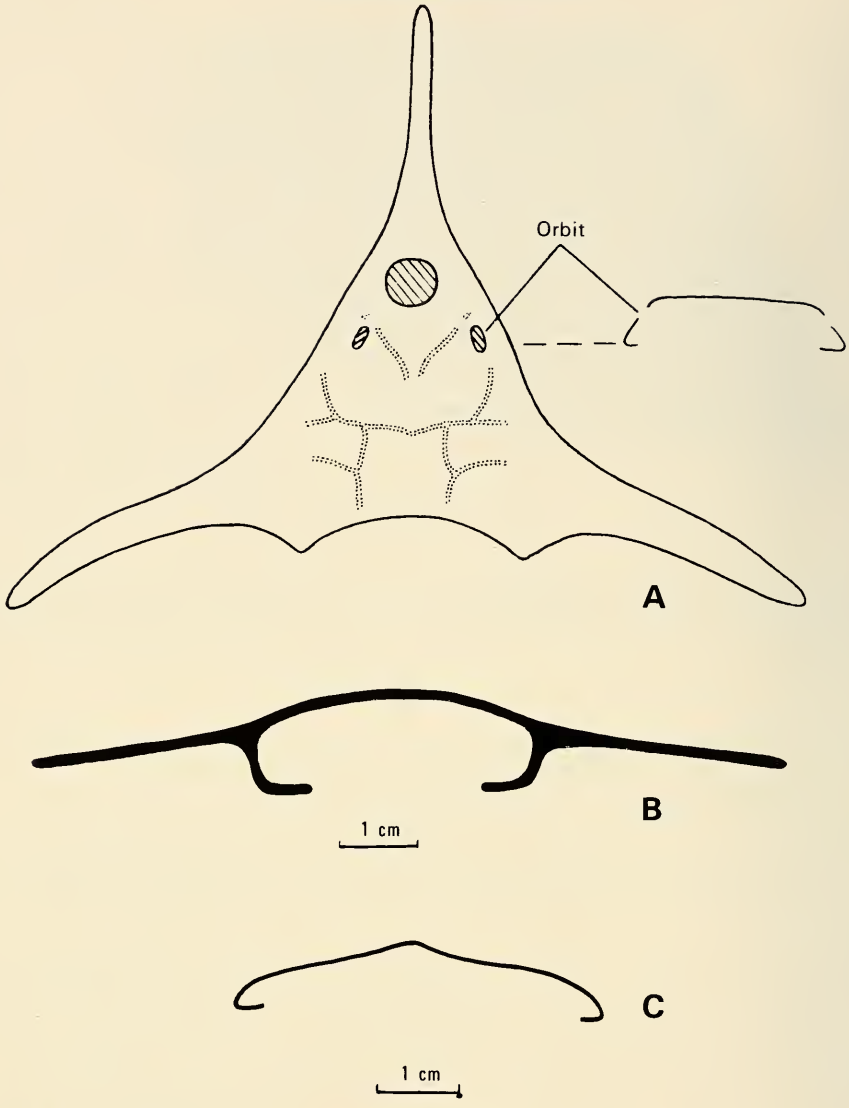

Fig. 3. **A, B.** *Asiaspis expansa* P'an. **A,** Cephalic shield in dorsal view, showing section through the orbital region (after V1314a, Museum of Geology, Beijing). **B,** section through the posterior part of the shield. **C,** *Polybranchiaspis liaojiaoshanensis* Liu. Section through the posterior part of the cephalic shield.

shields of a large polybranchiaspid were discovered in Late Devonian red sandstones in Ningxia, west China. These polybranchiaspids are associated with the antiarch *Remigolepis*, and are the youngest representatives of the group so far known from China.

Discussion

As the eugaleaspidomorphs are unlike any previously described agnathans, their relationships to the other known major groups have become a subject of controversy (Liu, 1975; Janvier, 1975; Halstead, Liu and P'an, 1979). The various groups possess

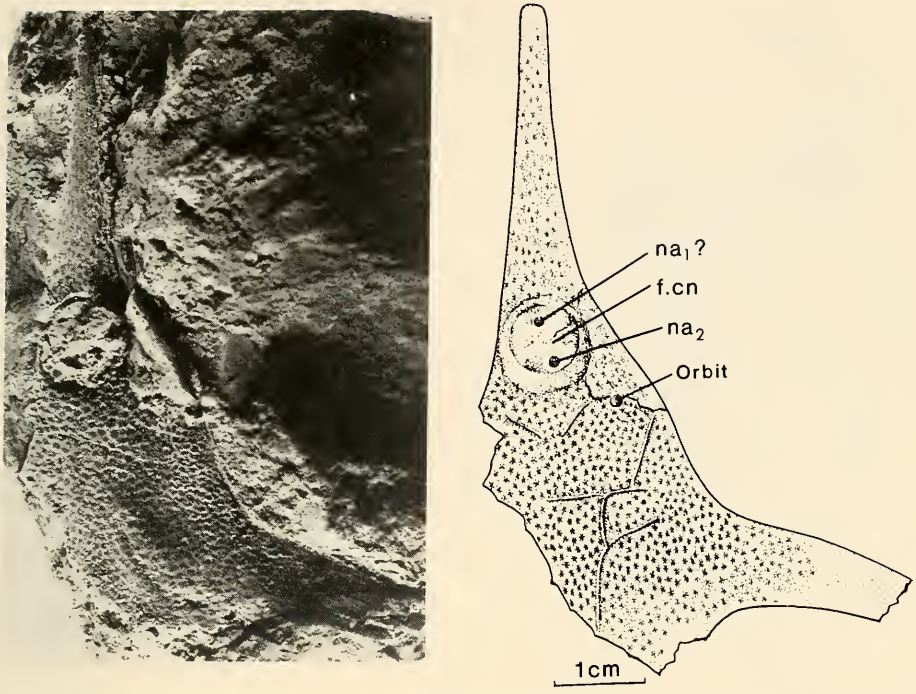

Fig. 4. Asiaspis expansa P'an. Headshield in dorsal aspect (V1336, Museum of Geology, Beijing) *f.cn,* circumnasal fossa; na_1, opening of hypophysial duct; na_2, nasal opening.

a bony carapace covering the anterior part of the body dorsally and laterally, as in osteostracans. Their three main dorsal openings on the cephalic shield, and separate gill openings, may be regarded as specializations shared with osteostracans and anaspids. The most controversial structure is the dorsal median opening. This has been observed in many new fossils discovered in south China since 1965 (e.g. *Sinogaleaspis, Yunnanogaleaspis, Sanchaspis, Kwangnanaspis, Hanyangaspis,* etc.). The dorsal median opening was first interpreted as a naso-hypophysial opening in *Eugaleaspis* (very long, slit-like in form) by comparison to that of the Cephalaspidomorphi, and as a mouth in *Polybranchiaspis,* comparable to that in some Heterostraci (Liu, 1965, 1973, 1975; P'an *et al.,* 1975: P'an and Wang, 1978; Cao, 1979).

Halstead *et al.* (1979) described small plates in *Polybranchiaspis* and *Galeaspis* which apparently covered the dorsal median opening in life. However, it is surprising that among more than two hundred excellently-preserved specimens of eugaleaspidomorphs recently collected in Yunnan, Guizhou (Kueichow), Sichuan (Szechuan), Guangxi (Kwangsi), Hunan, Hubei, Jiangxi (Kiangsi), Zhejian (Chekian), and Anhui (Fig. 1), no similar cover plate has been observed in position over the opening. It is my opinion that the dorsal median opening served as an inhalent nasohypophysial opening, and there is also evidence that very possibly this opened directly into the buccal cavity, as in hagfish (Myxinoidea). If this evidence and interpretation are correct, the retention of a naso-pharyngeal duct in eugaleaspidomorphs would be evidence against grouping them with the Cephalaspidomorphi.

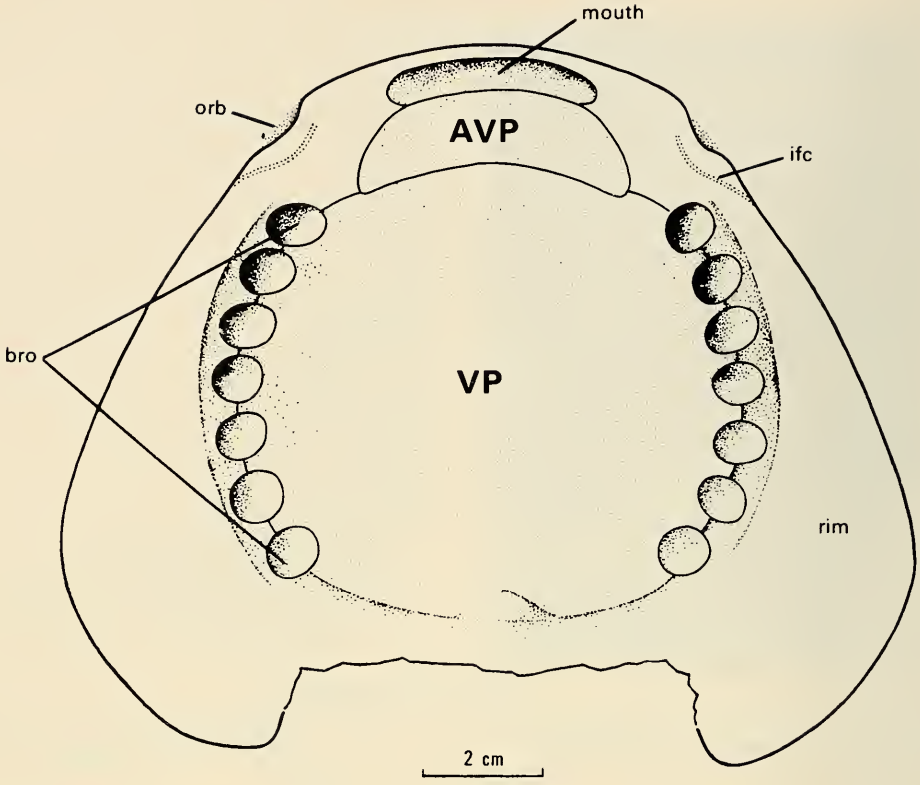

Fig. 5. Hanyangaspis guodingshanensis P'an and Liu. Articulated specimen in ventral view, showing the circular ventral shield replacing the zone of polygonal tesserae. Other features are the seven branchial openings, the shape of the anteroventral plate, and the broad ventral rim (VH001, Museum of Geology, Beijing). *AVP,* anteroventral plate; *bro,* external branchial opening; *ifc,* infraorbital sensory canal; *orb,* orbit; *VP,* ventral shield.

Recently two very small tubes have been discovered within the dorsal median opening of *Asiaspis expansa* (P'an *et al.,* 1975: pl. 6, fig. 2). The anterior one is interpreted as the opening of the hypophysial duct or pharyngeal duct (na_1?, Fig. 4), and the posterior one as a nasal opening proper (na_2). The dorsal median opening is termed a circumnasal fossa *(f.cn).* In addition, in this specimen there is no visible pineal opening between the orbits.

Under this interpretation the inner margin of the rostral ventral rim marks the anterior margin of the mouth, as in cephalaspids and some heterostracans. This region is preserved in many new specimens (e.g. *Hanyangaspis guodingshanensis* P'an and Liu, *Dongfangaspis* spp., *Polybranchiaspis* sp., and some new genera from south China). The anterior margin of the antero-ventral plate or ventral shield must have marked the posterior margin of the mouth in eugaleaspidomorphs (Fig. 5).

The internal anatomy of the eugaleaspid carapace is now well known. The round structure arising from beneath the anterior and posterior semi-circular canals and situated between them and the brain in *Duyunolepis* may be interpreted as the sacculus (see Halstead, 1979: fig. 3).

Each branchial chamber (gill pouch) is associated with a separate branchial

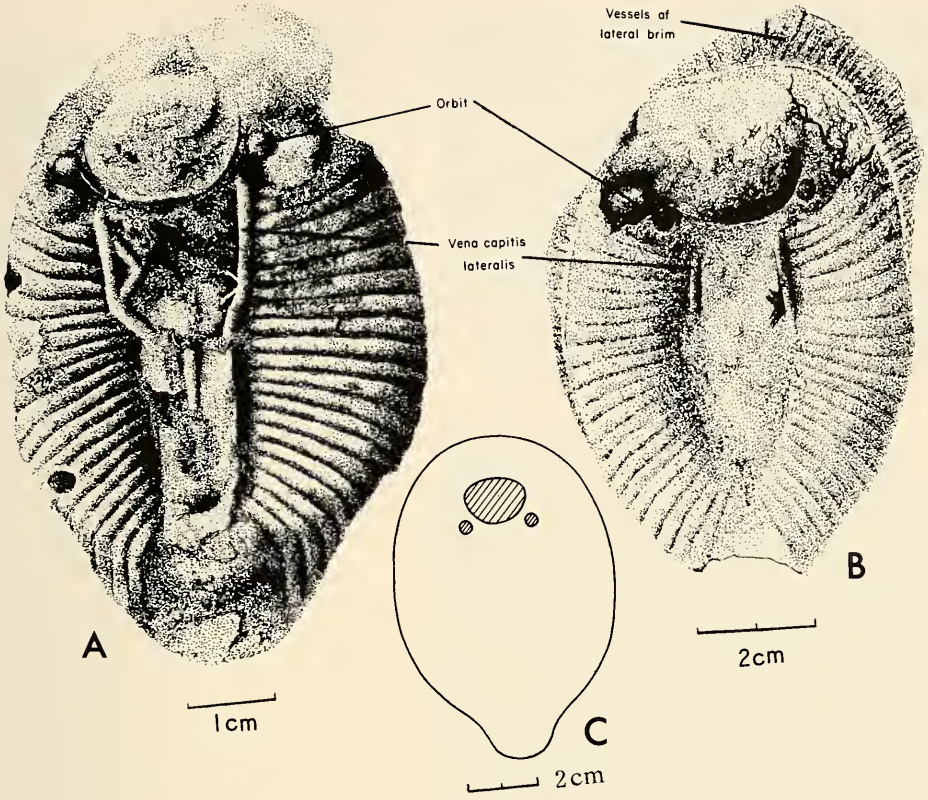

Fig. 6. Duyunolepis ('Duyunaspis') paoyangensis (P'an and Wang). Casts of the internal cavities and canals of the cephalic shield in dorsal view. **A**, VG001; **B**, VG002 (Museum of Geology, Beijing). Early Devonian, lowermost part of the Shujiapin Formation, Paoyang, Duyu, Guizhou (Kueichow) Province. **C**, sketch of cephalic shield in dorsal view, showing position of the orbits adjacent to the posterolateral margins of the dorsal median opening.

opening along the ventrolateral margin of the cephalic shield in *Asiaspis, Polybranchiaspis, Hanyangaspis,* and *Duyunolepis.* Markings on the undersurface of the dorsal shield have been interpreted by Liu Yuhai, Wang Shitao, and the author as representing the former position of the upper parts of branchial chambers, but alternatively they were regarded as 'somites or segmental muscle blocks' by Halstead (1979: 836). In the author's opinion these structures can be best interpreted as the upper parts of the branchial chambers.

The positions of the nasal sacs and lobes are more difficult to decide, but in all known jawless vertebrates, the olfactory organ is never very far from the telencephalic division of the brain cavity. It would thus be more appropriate to consider the olfactory organ of *Duyunolepis paoyangensis* and *Paraduyunaspis hezhangensis* as situated in the posterior part of the recess surrounding the naso-hypophysial cavity, as already proposed by P'an and Wang (1978). An alternative interpretation by Halstead (1979: fig. 3) placed the nasal sac in the recess interpreted here as the orbit. Halstead's interpretation has been rejected by Janvier (1981), who supports our original interpretation (P'an and Wang, 1978) of the position of the nasal sac. However Janvier

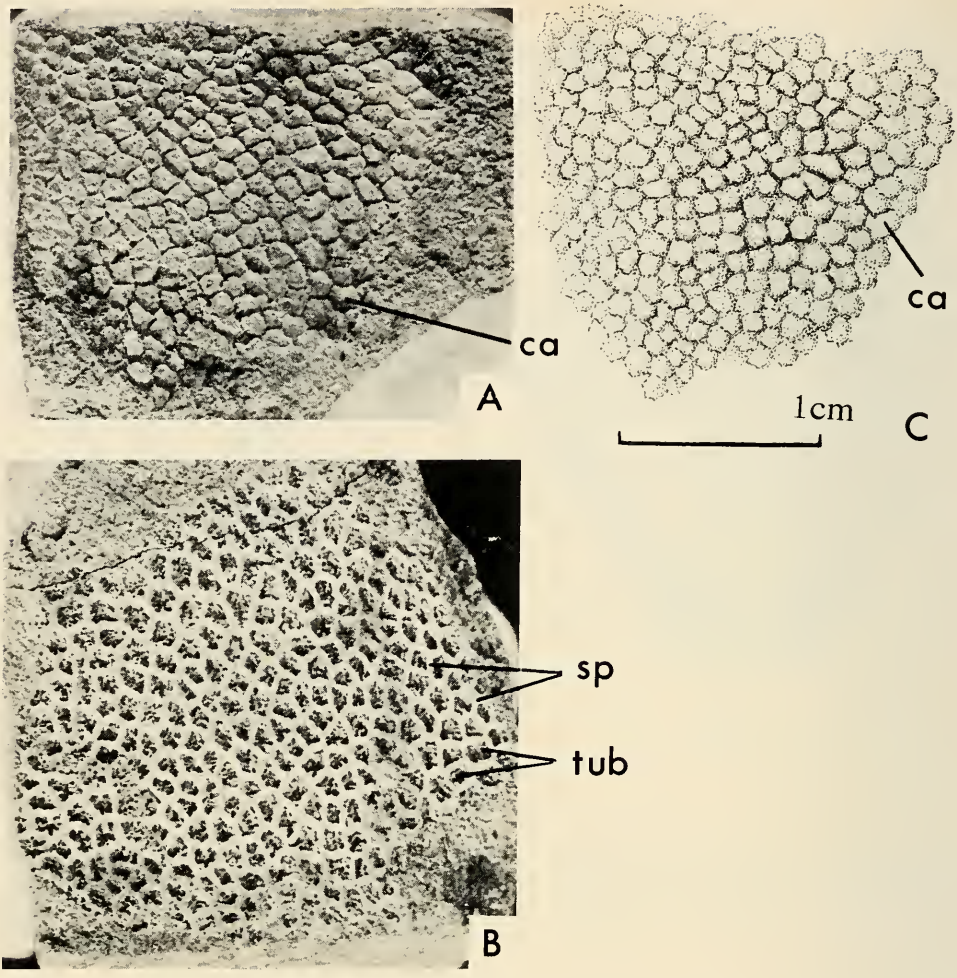

Fig. 7. Specimen showing the structure of the eugaleaspid exoskeleton (possibly *Sinogaleaspis* sp.). VJ001 (Museum of Geology, Beijing) from the Late Silurian-Early Devonian Xiking Formation, Xiking, Xiushui, Jiangxi Province. **A,** natural cast of the internal surface of a fragment; **B,** natural cast of the external surface of the same specimen, showing impressions of tubercles of the dermal ornament *(tub),* and the septa of honeycombs of the cancellous layer *(sp);* **C,** redrawn from photograph A, showing impressions of honeycomb structure of the cancellous layer *(ca).*

has followed Halstead (1979) in interpreting the 'lateral elevations' of P'an and Wang (1978: fig. 1, *pmic*) as the orbits. On the evidence of additional specimens (Fig. 6), it is maintained that the orbits of *Duyunolepis* are positioned adjacent to the posterolateral margins of the dorsal median opening, and thus in a somewhat different position to other genera (*Eugaleaspis, Polybranchiaspis, Hanyangaspis, Huananaspis,* etc.). Halstead (1979) also reinterpreted the canal first identified (P'an and Wang, 1978) as for a branch of the vagus nerve. According to Halstead this canal contained the dorsal aorta, but there are arguments against this (Janvier, 1981: 147). This paired canal, which runs posterolaterally from the myelencephalic division of the brain cavity along the inner side of the branchial chambers, is best interpreted as for a branch of the vagus nerve (X).

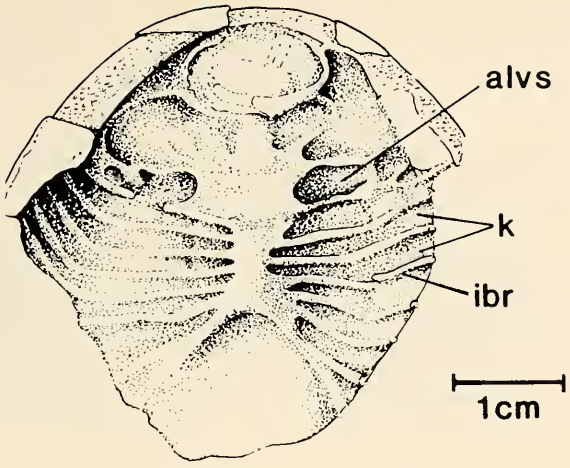

Fig. 8. Polybranchiaspis liaojiaoshanensis Liu. Internal view of head shield (V3027, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing). *alvs,* anterior sinus for vena capitis lateralis; *k,* position of the dorsal part of the branchial fossae; *ibr,* interbranchial ridge. (modified after Halstead, 1979: fig. 1).

By comparison, the position of the anterior sinus for the vena capitis lateralis in *Polybranchiaspis liaojiaoshanensis* (Fig. 8) is in the region labelled 'internal nasal fossa' and 'internal nostralis' by Liu (1975: fig. 5C). The 'internal nostralis' is more difficult to identify, but the position of the sinus is likely to be adjacent to the anterior part of the branchial area, and rather as in *Duyunolepis paoyangensis* and *Paraduyunaspis hezhangensis* (P'an and Wang, 1978: 300-311, figs 1-5, pls 27, 37).

Some very fine ridges occur around the dorsal median cavity (opening) in the holotype of *Paraduyunaspis hezhangensis* (see P'an and Wang, 1978: 307-309, figs 4, 5, pl. 27, fig. 4), which supports the interpretation of the dorsal median cavity as an olfactory organ, with these ridges (Fig. 9) representing traces of the olfactory epithelium. This would be rather as in Heterostraci (e.g. Janvier, 1981: fig. 12D), but there is no evidence in this specimen as to whether this cavity opened directly into the buccal cavity or not.

As already pointed out, the eugaleaspidomorphs, Osteostraci, and Anaspida all have separate gill openings and three main dorsal openings on the head. Considering also the well ossified cephalic shield, there is an apparent similarity between eugaleaspidomorphs and the Osteostraci, with the exception of the presence of dorsal and lateral sensory fields and a pineal opening in the latter.

Features which appear to link the eugaleaspidomorphs with the heterostracans include a simple brain, pineal body covered by the external armour, and a very large ventral shield. In addition, the middle layer of the exoskeleton is very similar to the cancellous layer (honeycomb structure) in that of the Heterostraci (Fig. 7).

The phylogeny of eugaleaspidomorphs is still relatively obscure, mainly because of the uncertainty as to their sister group (Janvier, 1981: 148, fig. 14D-F). In the author's opinion, the various eugaleaspids and polybranchiaspids possessed a combination of osteostracan and heterostracan features (Stensiö, 1964, 1968). They are neither typical Cephalaspidomorphi nor true Pteraspidomorphi. To conclude, the author believes that the hanyangaspid, eugaleaspid, polybranchiaspid, nanpanaspid, duyunolepid, huananaspid, and other new Chinese groups can be united into a single major high-rank taxon, the Eugaleaspidomorphi, equivalent in status to the Cephalaspidomorphi and to the Pteraspidomorphi.

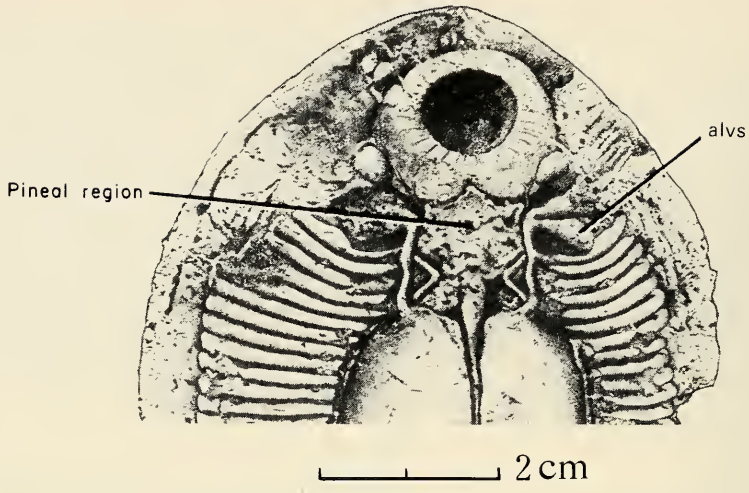

Fig. 9. Paraduyunaspis hezhangensis P'an and Wang. Anterior part of a cast of the internal cavities and canals of the cephalic shield in dorsal view, showing fine ridges around the opening of the dorsal median cavity (holotype, V1543, Museum of Geology, Beijing). *alvs,* anterior sinus for vena capitis lateralis.

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